Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA

Julio L. Betancourt [a],[*], Kate Aasen Rylander [a], Cristina Peñalba [b], Janet L. McVickar [c]

[a] *US Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745, USA*
[b] *Instituto de Ecologia, UNAM, A.P. 1345, Hermosillo Sonora, Mexico*
[c] *National Park Service, PO Box 728, Santa Fe, NM 87504, USA*

Abstract

South-central New Mexico, USA, at the junction of the Rocky Mountains, High Plains and Chihuahuan Desert, is one of the better known regions in the late Quaternary of North America. Plant macrofossils and pollen from a packrat midden series in Rough Canyon, New Mexico allows refinement of plant distributions and paleoclimates in this transitional area since full glacial times. From 17 000 to 12 000 ^{14}C yr BP, *Pinus edulis–Juniperus scopulorum* woodlands dominated limestone substrates between 1800 and 1490 m, with *Pseudotsuga menziesii* and other mixed-conifer species restricted to shady, north-facing slopes. *Juniperus deppeana*, the dominant juniper today above 2000 m in southern New Mexico, is conspicuously absent from glacial middens and must have been displaced south of the US–Mexico border. The minimum climatic conditions for *P. edulis–J. scopulorum* woodlands are ca 20% wetter and 3.5–5°C cooler (July mean maximum temperatures) than the modern climate at Rough Canyon. Holocene warming/drying may have started as early as 12 000 ^{14}C yr BP with the extirpation of *J. scopulorum* from Rough Canyon, and was completed by at least 10 540 ^{14}C yr BP. The record for arrivals of some desert species is confounded by traces of pollen and macrofossils in some of the glacial middens, which could signify either earliest occurrence or temporal mixing (contamination) of assemblages. AMS ^{14}C dating can discriminate between early arrival and contamination in midden macrofossils but not in pollen. AMS dates show that *Choisya dumosa*, presently near its northern (cold) limits at Rough Canyon, endured late glacial winters, possibly as clonal populations. Some *Larrea tridentata* leaves and pollen occur in middens dominated by conifers and oaks no longer at the site; an AMS date of 3205 ^{14}C yr BP on *Larrea* leaves from one midden indicates contamination. Evidence for some macrofossil contamination, however, does not rule out the possibility that pollen of desert elements (e.g. *Larrea*, *Prosopis*) in late glacial–early Holocene middens indicates their presence in the Tularosa Basin, well ahead of their local appearance in Rough Canyon. Finally, the increasing dominance of desert elements after 5000 ^{14}C yr BP in the Rough Canyon series and elsewhere in the northern Chihuahuan Desert could reflect slow, postglacial migration from the south and/or progressive encroachment with gradual stripping of soils formed during the last glacial period. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Chihuahuan Desert; climate change; Holocene; macrofossils; packrat middens; paleoecology; Pleistocene; pollen

* Corresponding author. Fax: +1-520-670-6806.
E-mail address: jlbetanc@usgs.gov (J.L. Betancourt)

1. Introduction

This report focuses on plant macrofossil and pollen analyses of 30 packrat (*Neotoma*) middens spanning the last 17 000 ^{14}C yr from Rough Canyon, south-central New Mexico (Figs. 1 and 2). The midden record complements paleoenvironmental studies at Pendejo Cave, a controversial
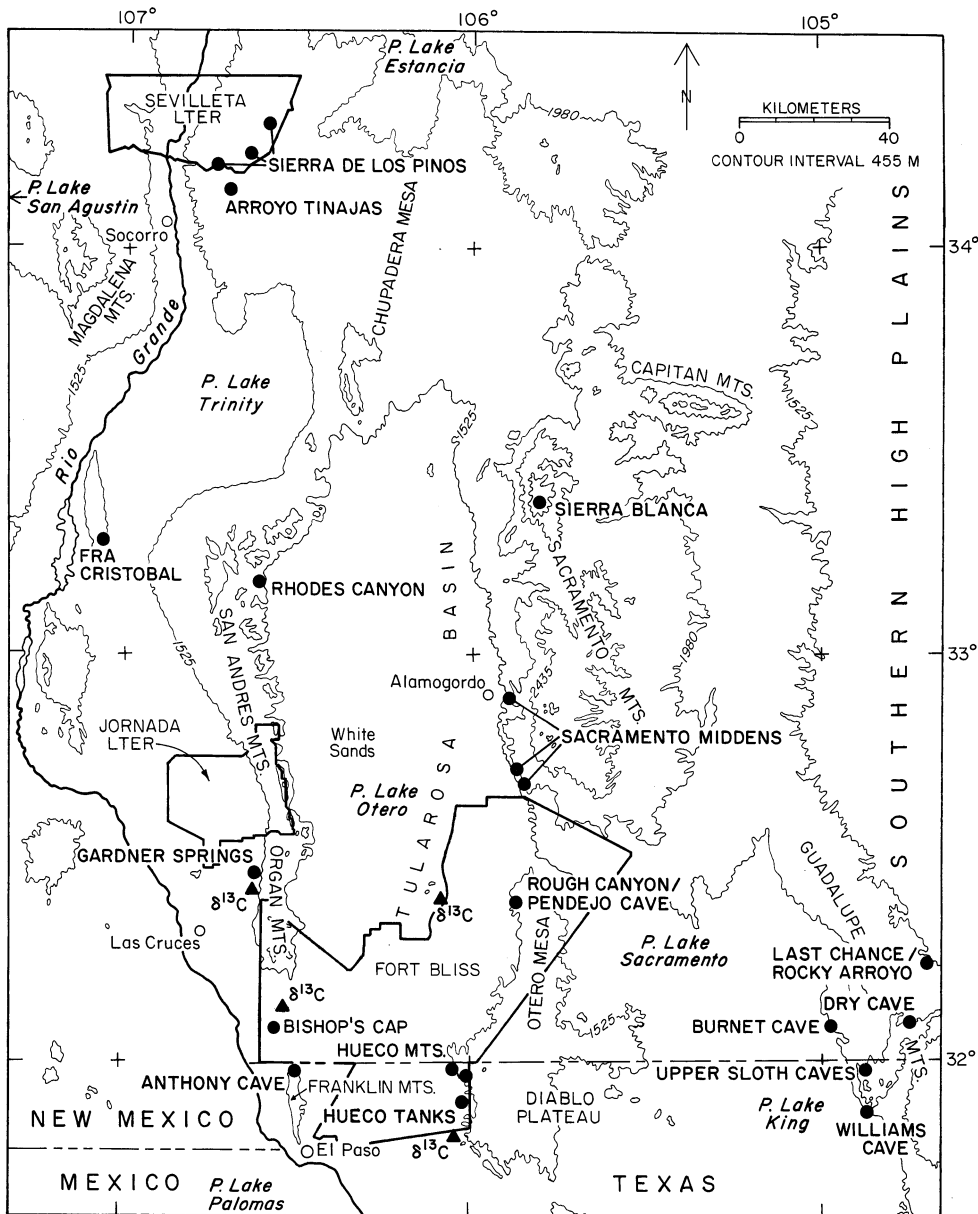

Fig. 1. Map of northern Chihuahuan Desert, showing location of major paleoenvironmental study sites. Contour intervals were converted from feet to meters base 1:500 000 state maps for Texas and New Mexico. δ^{13}C denotes sites where carbon isotopes were analyzed from soil carbonates by Cole and Monger (1994); Monger et al. (1998) and Buck (1996) to infer the proportion of C_3/C_4 biomass during the late Quaternary. Closed circles denote midden sites.
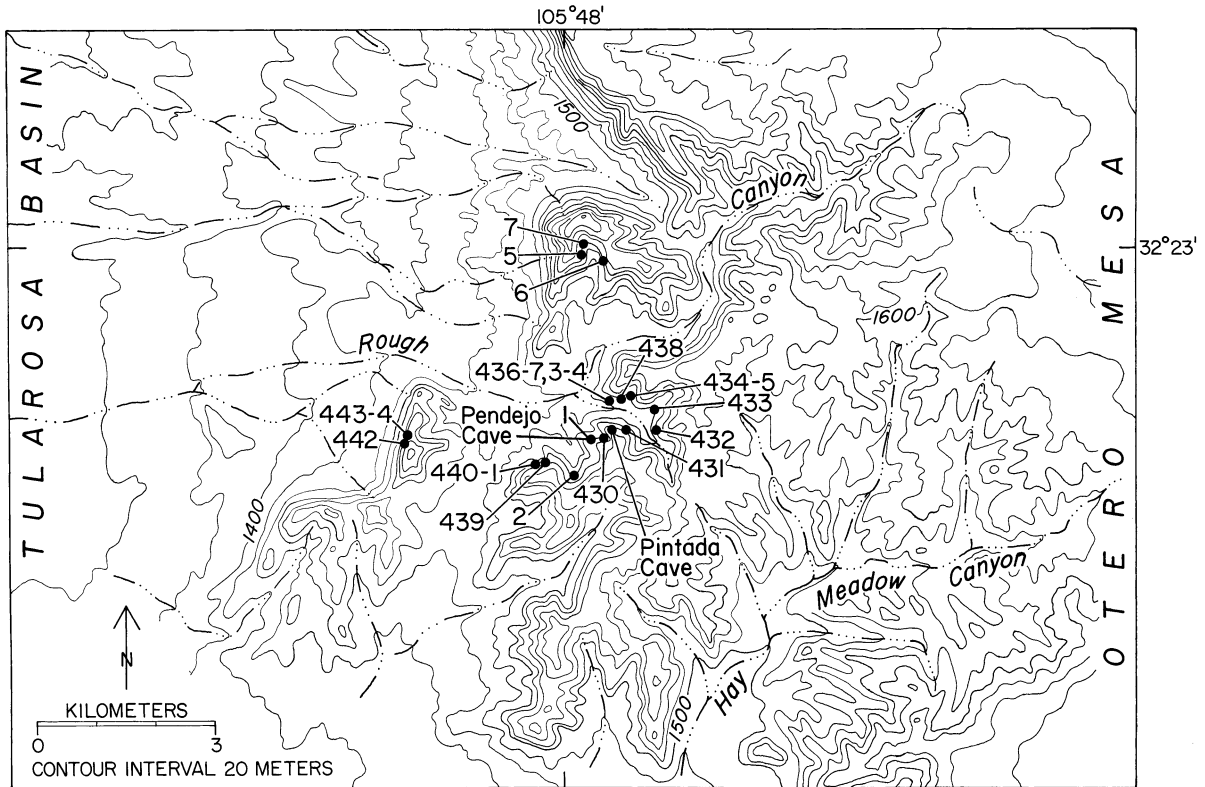
Fig. 2. Map of Rough Canyon showing location of fossil packrat midden sites and Pendejo Cave.

'pre-Clovis' site located in the same canyon (Harris, 1995; Chrisman et al., 1996). Pendejo Cave sediments incorporate abundant plant and animal remains spanning the last 50 000 ^{14}C yr; the cave sediments in large part represent loose debris accumulated by packrats. The controversy revolves around the stratigraphic integrity of the cave sediments, and presumed human friction skin prints on clay nodules and other putative human artifacts from stratigraphic layers that are of pre-Clovis (> 11 500 ^{14}C yr BP) age (Chrisman et al., 1997a,b; Dincause, 1997; Shaffer and Baker, 1997). The Rough Canyon packrat middens overlap with Pendejo Cave sediments from the full to the late glacial, but represent better coverage in the Holocene.

Rough Canyon and Pendejo Cave are 50 km north and south of two other midden studies along the nearly continuous western escarpment of the Sacramento (Van Devender et al., 1984) and

Hueco Mountains (Van Devender, 1990a,b), respectively. The Hueco Mountain series (42 middens; last 40 000 yr) comes from 1340 to 1440 m, whereas the Sacramento series (13 middens; last 18 000 yr) was sampled between 1555 and 1690 m. The Rough Canyon series (last 17 300 ^{14}C years) is intermediate in elevation (1490–1579 m), allowing unique resolution of former plant distributions along a key elevational range that today defines the upper (and northern) limits of many Chihuahuan desert plants. Key biogeographic issues that are addressed with the Rough Canyon midden series include: (1) exact lower limits on limestone for conifers such as *Pseudotsuga menziesii* and *Juniperus scopulorum* during the last glacial age; (2) identification and precise ranges for key pinyon and juniper taxa in glacial-age woodlands; (3) the importance of sagebrush (*Artemisia tridentata*-type) steppe vs. C_4 grasses in rocky vs. deep soils of the Tularosa Basin during the late glacial

period; (4) timing for Holocene arrival of dominant shrubs at higher elevations in the northern Chihuahuan Desert. Key paleoclimatic questions are: (1) synchroneity of major climatic changes in late Quaternary of the northern Chihuahuan Desert; (2) improved estimates for magnitude of temperature and precipitation (amounts and seasonality) shifts during the last deglaciation; (3) evaluation of mid-Holocene climate at a site clearly dominated by monsoonal circulation and precipitation.

2. Previous work

Paleoenvironmental research in south-central New Mexico (see Fig. 1) has involved: (1) mapping and dating of shorelines and the geochemistry and limnology of pluvial lake sediments (Lake Estancia: Bachhuber, 1971, 1989; Bachhuber and McClellan, 1977; Allen and Anderson, 1993; Lake San Agustin: Markgraf et al., 1984; Phillips et al., 1992; Lake Trinity: Neal et al., 1983; Lake Otero: Herrick, 1904; Lake Sacramento: Hawley, 1993; Wilkins and Currey, 1997; Lake King: Boyd and Kreitler, 1986; Wilkins and Currey, 1997; Lake Palomas: Reeves, 1969; see regional summary by Hawley, 1993); (2) interpretation of glacial deposits on Sierra Blanca, the southernmost Pleistocene glaciers in the US (Richmond, 1962, 1986), as well as rock glaciers in the San Mateo (Blagbrough, 1986) and Sacramento Mountains (Galloway, 1983; Blagbrough, 1984, 1991); (3) soil geomorphological studies affiliated with the Desert Project (Gile et al., 1981), which laid the necessary groundwork for stable isotopic analyses of soil carbonates (Cole and Monger, 1994; Buck, 1996; Monger et al., 1998); (4) a variety of spring deposits exploited for pollen (Freeman, 1972) and mollusks (Metcalf, 1977); (5) a rich record of Pleistocene vertebrates from cave deposits (Harris and Findley, 1964; Smartt, 1977; Thompson et al., 1980; Logan, 1981; Harris, 1984, 1985, 1987, 1989, 1995; Connin et al., 1998); (6) paleoecological analyses of 227 ^{14}C-dated packrat middens (Van Devender, 1977, 1980, 1990a; Van Devender and Everitt, 1977; Van Devender et al., 1979, 1984, 1987; Van Devender and Riskind, 1979; Van

Devender and Toolin, 1983; Betancourt et al., 1990; Elias, 1992; Elias and Van Devender, 1992; Thompson et al., 1993; Betancourt et al., 1993; this report); and (7) paleoenvironmental studies as background for Paleoindian adaptations, incipient agriculture, and subsequent changes in settlement pattern (Bohrer, 1981; Wills, 1988; Haynes, 1991, 1995; Chrisman et al., 1996; Tagg, 1996).

The Tularosa Basin has unusual densities of Folsom sites associated with small, temporary playas. It has long been speculated that Folsom and other Paleoindian perishables might turn up in the numerous limestone caves overlooking the Basin. One such prospect is Pendejo Cave, located in Rough Canyon, a small embayment in the Otero Mesa Escarpment on McGregor Missile Range, Ft. Bliss Military Reservation. In 1991 and 1992, R.S. MacNeish and colleagues excavated the cave; much of the cave sediment represents massive deposition of packrat debris during the last 50 000 ^{14}C yr.

Paleoecological results for Pendejo Cave are summarized by Chrisman et al. (1996), including an analysis of bones by Harris (1995), pollen and plant macrofossils recovered through flotation (Gish, J., unpublished data), and plant macrofossils recovered from in-situ screening of excavated sediments (Hiles, H., unpublished data). Harris (1995) identified several extinct species [*Equus* spp. (horse), *Capromeryx* (midget goat) *Stockoceros*, *Coragyps occidentalis* (western vulture), *Hemauchenia*, *Camelops* (camel), and *Aztlanolagus agili*s (hare)] and made some preliminary inferences about climate and vegetation, mostly on the basis of extant species [specifically *Gopherus agassizi* (desert tortoise), *Sigmodon hispidus* (hispid cotton rat), *Geococcyx* spp. (California condor), *Sylvilagus* spp. (cottontail), *Neotoma cinerea* (bushy-tailed woodrat), *Marmota flaviventris* (marmot), *Microtus mexicanus* (Mexican vole), and *Lagurus curtatus* (sagebrush vole)]. Harris inferred cooler summers and a higher effective moisture than today through most of the glacial period (Isotope Stages 2 and 3), with warmer winters than today in the full and late glacial periods. Of interest is the presence of *Neotoma cinerea* throughout Pleistocene sediments at Pendejo Cave and other caves throughout the

region (Harris, 1984). The southern limit of this woodrat or packrat today is northern New Mexico. Apparently, *Neotoma cinerea* extended well into Chihuahua, Mexico during the Pleistocene and was probably responsible for much of the Pleistocene midden record in south-central New Mexico.

Plant macrofossils from flotation samples yielded *Pinus edulis* and *Juniperus* sp. (no species given) throughout the Pleistocene sediments of Pendejo Cave (Gish, J., unpublished data). Pinyon pollen ranged from 3 to 36%, and juniper from 1 to 32.5% of the total pollen count. Gish also found *Pseudotsuga menziesii (* Douglas fir) pollen and needles, indicating that it was growing at the site. Grass pollen frequencies are highest in the Holocene sediments, exceeding 15%, while grass contributes less than 10% in all of the glacial-age sediments. The presence of *Prosopis* (mesquite) leaves and pods throughout glacial-age cave sediments suggests temporal mixing through rodent burrows, roof fall events and other disturbances. The midden series reported here for Rough Canyon and nearby tributaries complements paleoecological studies at Pendejo Cave by replicating the glacial part of the record, providing extensive coverage during the Holocene and resolving questions about contamination in the cave sediments.

3. Physical setting

3.1. Geology

Rough Canyon and the Otero Mesa Escarpment are part of the Sacramento Mountain cuesta complex described by Hawley (1993). The complex is typified by high mesas, cuesta-form mountains with east-tilted dipslopes, west-facing escarpments (e.g. the Sacramento and Guadalupe Mts), and widely scattered structural basins (e.g. the Salt Basin formerly occupied by Pleistocene Lake King) (Fig. 1). The dipslopes are underlain by Paleozoic limestones, sandstones and shales interbedded with gypsum. The largely carbonate terranes dissolve into large karst depressions and expansive cave systems such as Carlsbad Caverns. The layered-

cake bedrock stratigraphy is exposed along the prominent west-facing escarpments, which rise abruptly from the floors of the Tularosa and Salt Basins at ca 1200 and 1300 m, respectively. The basin floors contain numerous intermittent playas, which coalesced in the last glacial period to form permanent lakes. Evaporites (gypsum) from Pleistocene Lake Otero in the Tularosa Basin are the source of the White Sands, the largest dune field in New Mexico. The primary bedrock along the Otero Mesa Escarpment and in Rough Canyon is the Permian Yeso Formation, a 350–550 m thick complex of limestones, dolomites, shales, silt-stones, evaporites and fine-grained sandstones (Pray, 1961). In the Sacramento Mountains, the contact between the Yeso and the overlying San Andres Formation is a zone of water accumulation that produces springs wherever exposed at the land surface. The Yeso Formation also is pocked with caves, crevices and rock shelters ideal for packrat midden preservation.

3.2. Modern climate and vegetation

Climatic gradients in the area around Rough Canyon are well described by an elevational transect of weather stations from the lowland desert of the Tularosa Basin into the forested zone of the Sacramento Mountains (Table 1). Temperature decreases and precipitation increases linearly with elevation, except for minimum temperatures. which are generally inverted in the Tularosa Basin (White Sands and Orogrande). The modern climate for Rough Canyon (1490 m) was estimated by simple regression using five weather stations from 1380 to 2680 m (Table 1). The mean annual precipitation was estimated at 340 mm, with 50% occurring in the three wettest months of July, August and September. Highly variable precipitation in winter stems from the southerly position of the study area (32°N) relative to the mean position (45°N) and variability of the jet stream and the winter storm track over western North America (Bartlein et al., 1998). The subtropical jet also can entrain tropical Pacific moisture in winter, producing wetter winters and less arid foresummers (May–June) during El Niño years (1905, 1915, 1941, and after 1976). Highly variable

Table 1
Mean monthly maximum (T_{max}) and minimum (T_{min}) temperatures and mean annual precipitation (MAP) at different elevations in the Tularosa Basin and Sacramento Mountains[a]

Station	Elevation (m)	Jan T_{max} (°C)	Jan T_{min} (°C)	July T_{max} (°C)	July T_{min} (°C)	MAP (mm)
White Sands	1220	13.8	5.4	36.1	17.7	227
Orogrande	1280	14.1	2.8	35.3	18.7	258
Alamogordo	1326	13.5	1.9	34.7	16.9	292
Rough Canyon	1490	12.6	2.3	32.9	16.1	340
Mountain Park	2050	9.4	3.7	27.2	13.4	495
Cloudcroft	2680	5.5	7.1	22.9	8.7	672

[a] Fifty per cent of MAT at all stations occurs in the three wettest months of July, August, and September. Modern values for the Rough Canyon midden sites were estimated from elevation by simple regression using the actual weather stations.

cool seasons, dry foresummers, dominance of monsoonal rain, and occasional, extreme summer drought (1950–1956) are evident in a three-dimensional graph of historical precipitation at Orogrande, only 10 km west of Rough Canyon (Fig. 3).

Vegetation changes considerably from the valley floor of the Tularosa Basin, across the broad pediment of the Otero Mesa escarpment, into the cliffside and canyon bottom communities of Rough Canyon, and onto the grasslands of Otero Mesa proper (Kenmotsu, 1977; Fig. 2). The valley floor of the Tularosa Basin below ca 1240 m is dominated by *Prosopis glandulosa* (honey mesquite), *Atriplex canescens* (four-wing saltbush), *Gutierrezia sarothrae* (snakeweed), *Artemisia filifolia* (sand sagebrush) and *Yucca elata* (soaptree yucca) on coppice dunes, interdune areas and salt flats. The alluvial fan, a broad, gentle slope between 1250 and 1300 m, is covered primarily by *Larrea tridentata* (creosote bush) and *Flourensia cernua* (tarbush) with a patchwork of *Acacia*
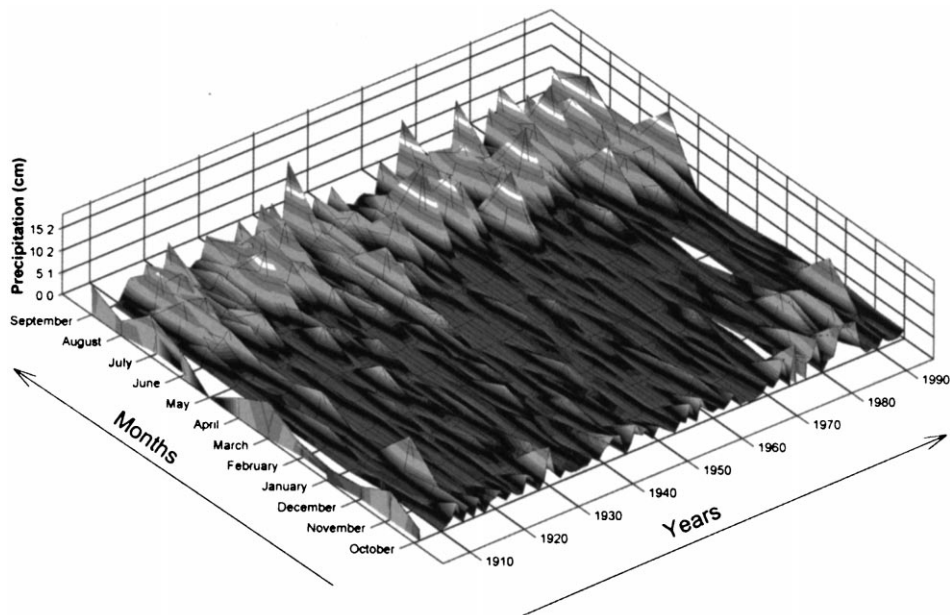

Fig. 3. Three-dimensional time series plot of monthly precipitation (1853–1995) from Orogrande, New Mexico, 10 km east of Rough Canyon.

constricta (catclaw), *Parthenium incanum,* and *Fouquieria splendens* (ocotillo) where soils and topography vary. A mixed-scrub community occupies the gravelly slopes and steep, rocky terrain along the escarpment between 1300 and 1600 m. Common species include *Larrea tridentata*, *Fouquieria splendens*, *Dalea formosa* (feather indigobush), *Parthenium incanum*, *Viguiera stenoloba* (goldeneye), *Glossopetalon spinescens* (spiny greasebush), *Koeberlinia spinosa* (allthorn), *Ceratoides lanata* (winterfat), *Opuntia imbricata* (tree cholla), *O. violacea* (purple prickly pear), *O. engelmannii (* Engelmann prickly pear), *Yucca torreyi* (torrey yucca), *Y. elata*, *Ephedra* spp. (joint fir), and *Acacia constricta*. Dry south-facing slopes in Rough Canyon, support large patches of *Acacia constricta*, *Prosopis glandulosa*, *Opuntia engelmannii* and *O. violaceae*. Cliffside communities include *Petrophytum caespitosum* (rock mat) *Notholaena sinuata* (wavy cloak fern), and *Cheilanthes* spp. on exposed rock surfaces, with *Berberis trifoliolata* (agarito), *Rhus trilobata* (squaw bush), *Aloysia wrightii* (bee brush), and *Choisya dumosa* restricted to shady, north-facing slopes. North-facing slopes in the reach from Pendejo Cave to RC 432 (Fig. 2) also have the greatest and most diverse grass cover. The grass flora of Rough Canyon includes *Bouteloua gracilis* (blue grama), *B. eriopeda* (black grama) *B. curtipendula* (side-oats grama), *Muhlenbergia porteri* (bush muhly), *Sporobolus* spp. (dropseed), *Aristida* spp. (three-awn), *Erioneuron pulchellum* (fluff grass), *Leptochloa dubia* (green spangletop), *Lycurus phleoides* (wolftail), *Oryzopsis hymenoides* (Indian ricgrass)*, Bothriochloa* sp. (beardgrass), *Schizachyrium scoparium* (little bluestem), *Scleropogon brevifolius* (burro grass), *Heteropogon contortus* (tangle head), *Tridens muticus* (slim tridens), and *Stipa neomexicana* (New Mexican feathergrass). Both oaks and junipers are scarce in Rough Canyon; a lone juniper (*Juniperus coahuilensis*) is found along a steep drainage ca 75 m east of Pendejo Cave.

Otero Mesa is a vast expanse of short-grass prairie that dips gently, from 1600 m at the head of Rough Canyon to 1300 m, more than 30 km to the east (Figs. 1 and 2). Principal grasses on Otero Mesa include *Bouteloua* spp., *Sporobolus* spp., *Panicum obtusum* (vine mesquite), and *Hilaria mutica* (tobosa grass). Shrub communities on Otero Mesa are restricted to gravelly soils on the perimeter of the mesa and on arroyo terraces. These communities include *Larrea tridentata*, *Gutierrezia*, and *Parthenium incanum*. Washes on Otero Mesa are lined with *Chilopsis linearis* (desert willow), *Rhus microphylla*, *Brickellia laciniata*, *Viguiera stenoloba* and *Fallugia paradoxa* (Apache plume). Broad, unincised washes that drain east of the Otero Mesa escarpment contain large patches of *Yucca elata*.

Pinyon–juniper woodlands do not occur along the Otero Escarpment, but cover broad expanses in the Sacramento and Guadalupe Mountains to the north and east. Tree cover dominates rocky terrain, but summer-flowering (C_4) perennial grasses are pervasive on deeper, loamier soils. For example, *Bouteloua gracilis* constitutes 55–80% of the plant cover at the Fort Stanton Experimental Range in open pinyon–juniper woodlands at ca 1980 m, northeast of of Sierra Blanca (Pieper et al., 1971). *Pinus edulis* (Colorado pinyon) can be found as low as 1700 m on the north faces of steep canyons draining the west escarpment of the Sacramento Mountains. Both *Juniperus monosperma* and *J. coahuilensis* occur in this woodland, replaced by *J. deppeana* (alligator-bark juniper) at ca 2100 m. Both *J. coahuilensis* and *J. deppeana* are sprouters and recover quickly after fire. The dominance of *J. deppeana* in the upper elevation of pinyon–juniper woodland and lower elevations of ponderosa pine forest probably inhibits *J. scopulorum* (Rocky Mountain juniper), which occurs only rarely in both the Sacramento and Guadalupe Mountains. *J. scopulorum* replaces *J. deppeana* as the dominant high-elevation juniper at ca 34°N. *Pinus ponderosa* (ponderosa pine) parkland, with abundant *Quercus gambelii* (Gambel oak) and *Q. undulata* (wavyleaf oak), occurs from 2150 to 2500 m, where it is replaced by mixed-conifer forest dominated by *Pseudotsuga menziesii*, *Abies concolor* (white fir), *Pinus strobiformis* (southwestern white pine), *Picea pungens* (blue spruce), and *Populus tremuloides* (aspen). Spruce–fir forest is dominated by *Picea engelmanii* and *Abies lasiocarpa* (subalpine fir) above 2980 m and is best developed on the northeast slopes of

Sierra Blanca. Treeless alpine tundra occurs above 3640 m just north of Sierra Blanca.

4. Methods

4.1. Midden sampling and processing

Thirty-six middens spanning the last 17 000 ^{14}C yr were collected in Rough Canyon, 9 (RC1-7) by J.L. McVickar, in conjunction with the first excavations at Pendejo Cave in 1991, and 27 (RC 430–444) by J.L. Betancourt in 1996; of these 36 middens, only 30 were dated (Table 2).

One of the middens, RC1, came from Pendejo Cave itself, whereas the other midden localities are scattered throughout the canyon and nearby tributaries (Fig. 2). Each midden was extracted using a hammer and chisel, splits were made along clear stratigraphic units, and outside weathering rinds were removed by scraping with a chisel.

In the laboratory, midden samples were further examined for stratigraphic discontinuities, and split into discrete units when necessary. Again, any remnant of an outside weathering unit was removed with a chisel. The indurated, larger sample was weighed prior to soaking in a closed plastic bucket. For Rough Canyon middens,

Table 2
Site location and radiocarbon dates from Rough Canyon packrat middens

Midden	Latitude	Longitude	Elevation (m)	Slope	Mean age (^{14}C yr)	S.D.	Lab No.
RC4	N32°22.7′	W105°52.83′	1490	SW	17 300	190	Beta51634
RC4-14	N32°22.7′	W105°52.83′	1490	SW	15 760	190	Beta51230
RC3	N32°22.7′	W105°52.83′	1490	SW	13 230	60	Beta72561*
RC436	N32°22.7′	W105°52.83′	1490	S	12 910	220	GX21968
					12 590	70	GX23372*
RC444A	N32°22.39′	W105°54.07′	1500	W	11 820	200	GX21907
					2410	50	GX23373*
RC444C	N32°22.39′	W105°54.07′	1500	W	11 680	280	GX21908
RC430F	N32°22.62′	W105°52.85	1530	N	10 540	210	GX22040
RC435A	N32°22.7′	W105°52.83′	1510	SE	7610	180	GX22041
RC430E	N32°22.62′	W105°52.85′	1530	N	7010	170	GX22032
RC442B	N32°22.39′	W105°54.07′	1500	SW	6295	110	GX21969
					3205	70	AA21656*
RC430D	N32°22.62′	W105°52.85′	1530	N	6240	350	GX21965
RC430A	N32°22.612′	W105°52.85′	1530	N	5395	305	GX21964
RC440	N32°22.40′	W105°53.34′	1530	N	4750	215	GX22036
RC435D	N32°22.7′	W105°52.83′	1510	E	4525	125	GX22069
RC444B	N32°22.39′	W105°54.07′	1500	W	4510	150	GX21906
RC430B	N32°22.62′	W105°52.85′	1530	N	4015	105	GX22031
RC441	N32°22.40′	W105°53.33′	1530	N	3035	95	GX22037
RC443	N32°22.39′	W105°54.07′	1500	W	2885	100	GX21909
RC439	N32°22.40′	W105°53.34′	1530	N	2345	85	GX22035
RC442C	N32°22.39′	W105°54.07′	1500	SW	2160	125	GX21970
RC432	N32°22.62′	W105°45′	1520	S	2005	85	GX21966
RC5L	N32°23′	W105°48′	1579	S	1770	70	Beta51860
RC5U	N32°23′	W105°48′	1579	S	1650	70	Beta51861
RC438	N32°22.7′	W105°52.85′	1495	S	1285	95	GX22071
RC434	N32°22.7′	W105°52.83′	1510	S	1210	115	GX21910
RC435B	N32°22.7′	W105°52.83′	1510	SE	1035	75	GX22042
RC5	N32°3′	W105°48′	1579	S	990	60	Beta51859
RC433A	N32°22.7′	W105°45′	1510	S	930	105	GX21967
RC433B	N32°22.7′	W105°45′	1510	S	860	70	GX22034
RC431	N32°22.57′	W105°52.83′	1530	NE	200	80	GX22033

sample weights ranged from ∼300 to 1400 g. Disaggregation of the indurated samples in water normally takes 1–2 weeks. We purposefully avoided adding diluted HCl, which in the past has been used to hasten dissolution of heavily carbonated midden samples commonly encountered in limestone crevices. The acid denatures DNA fragments and may preclude genetic analysis of the plant and animal remains in the future; the acid can also destroy plant epidermis.

After disaggregation, the contents of the bucket were poured through a 0.833 mm (No. 20) standard testing sieve and gently wet-screened. The wet-sieved fraction was placed on a paper plate and dried in an oven at ∼66°C for ∼48 h. Packrat fecal pellets (0.76–11 g per midden) were set aside for ^{14}C dating. In addition, AMS dates were obtained from *Pinus edulis* needles from RC3 and *Larrea tridentata* from RC442B (Table 2) to test for contamination. Contamination by younger material happens when different stratigraphic units are mixed inadvertently or weathering rinds are not removed carefully. Contamination also happens because physical processes, such as rehydration and crystallization of packrat urine, can mix younger debris into an older deposit. Also, rock crevices and shelters tend to be dynamic environments with considerable bird, insect and mammal activity. Temporal mixing of midden material poses a challenge. Although this challenge can be met by AMS dating of various organic fractions in a midden, costs are generally prohibitive. For now, the most economical approach is to reserve AMS dating for specific items suspected of being contaminants or critical to interpretations (e.g. persistence of glacial-age plants into the Holocene, the occurrence of modern desert flora in glacial-age assemblages or the Holocene arrival of a key species in the region) (Van Devender et al., 1985). Contamination of midden pollen assemblages is probably more pervasive than in macrofossil assemblages. Pollen grains are not only smaller, but also more ubiquitous (and by virtue of being airborne, more mobile), than macrofossils (∼10^5–10^6 pollen grains/cc vs. 10^0–10^1 plant fragments/cc^{-1} of indurated midden) in middens. Windborne pollen can continue to accumulate in outer weathering rinds and in cracks of a crystallized, fossil

midden during periods of relatively high humidity when the rind is sticky (Thompson, 1985). Although weathering rinds are carefully removed before middens are sampled, low levels of pollen contamination probably cannot be totally avoided. Unlike in macrofossil assemblages, unusual plant associations and the timing of species arrivals/departures in midden pollen series cannot be confirmed by AMS dating. This is particularly probematical for entomophilous/zoophilous taxa that are usually underrepresented, which has stimulated debate (Davis and Anderson, 1987; Van Devender, 1988). For example, traces of *Cercidium* pollen in middens (lacking *Cercidium* macrofossils) older than 8910 yr BP from the Waterman Mountains, southern Arizona, USA, were interpreted by Anderson and Van Devender (1991), not as first appearances in the regional vegetation, but as younger contaminants adhering to midden surfaces. Conversely, a high percentage (>20%) of *Larrea* pollen in a 14 120 yr BP midden from Organ Pipe Cactus National Monument, southern Arizona, USA, antedating first appearance as macrofossils by 6000 years, was interpreted to mean that it was present in the late glacial regional vegetation (Davis and Anderson, 1987; Davis, 1990). An AMS date of 18 700 yr BP on *Larrea* leaves from a midden at Tinajas Altas (Van Devender, 1990b), only 150 km west of Organ Pipe, makes the pollen interpretation seem plausible. First arrivals based on midden pollen evidence can neither be dismissed out of hand nor taken at face value; they remain a matter of interpretation.

A random 50 g subsample was selected from each sample and sorted for macrofloral, bone and insect remains using a 35× zoom binocular stereoscope. Prior to sorting, the midden debris was screened through both 2 mm (No. 10) and 1 mm (No. 18) mesh screens to facilitate visual scanning of midden debris. More than 100 taxa were identified in the 30 middens, based on comparison with herbarium specimens and other reference collections. Another 95 macrofossil 'types' could be identified with further work.

At present, we note difficulty in discriminating between *Berberis trifoliolata* and *B. haematocarpa* (red barberry) seeds and leaf fragments, *Acacia constricta* and immature *Prosopis* spines,

Echinocactus and *Mammillaria* (pincushion cactus) spines, Asteracea achenes and leaves, and among the so-called 'toothed' junipers [e.g. *Juniperus monosperma* (one-seed juniper) vs. *J. coahuilensis*], and between *Pinus edulis* and *P. remota* (papershell pinyon). Because *P. remota* was identified in Pleistocene middens from the nearby Hueco Mountains (Lanner and Van Devender, 1981), we examined every needle and nut shell carefully. Stomatal row number, stomatal shape (a range of shapes from round to rectangular present within a single stomatal trough), placement of the stomate within the row (often at oblique angles), stomatal size, and number of resin canals (two as viewed in cross-section) appeared consistent with *P. edulis*. In contrast, *P. remota* needles are characterized by much smaller stomata of a more uniform oval shape, are sunken in narrower stomatal troughs, and are generally thinner than *P. edulis*. Rough Canyon pine needles were thick, although somewhat short in length. Pine nut shells from Rough Canyon, while somewhat thin in medial cross-section, thickened towards the poles of the seeds, as do those of *P. edulis*. The shell fragments examined from Rough Canyon were not uniformly thin as are those of *P. remota*.

As many as four species of junipers were encountered in the Rough Canyon middens. *Juniperus scopulorum*, a non-toothed leaf juniper, was found in abundance in the late glacial middens. Serrate-leaf junipers presented more of a problem in species identification. Several species of 'toothed' junipers occur today in southern New Mexico, including: *J. deppeana*, *J. coahuilensis*, *J. pinchottii*, and *J. monosperma*. Modern trees are often difficult to distinguish. Identification of fossil juniper twigs and seeds is even more problematical. Rough Canyon middens included three morpho-types of serrate junipers, each possibly representing a single species: *J. coahuilensis* (somewhat flattened leaves with stomates visible above the intersection of the overlying leaf or scale), *J. monosperma* (beaked leaf shape in plan view with no stomates visible above the intersection of the overlying leaf; strong epidermal striations and medium-to-long teeth), and possibly a few fragments of *J. osteosperma* in one sample. The serrate leaves of a few of the juniper twigs in RC4-14 were twice

as large (both length and width) as those in any of the other Rough Canyon samples. In addition, the individual leaves were flattened and spatulate, and exhibited several stomates near the bottom of each leaf; these features are characteristics of *J. osteosperma*. An identification of *J. osteosperma* from the glacial period of south-central New Mexico is inconsistent with its modern distribution (mostly Great Basin and Colorado Plateau). This identification is very tentative, however, and further discrimination of junipers in Rough Canyon and at midden sites throughout west Texas and New Mexico is in progress. We did not identify *J. deppeana* from any of the middens, nor has it been identified from Pleistocene deposits anywhere in the Southwest. We feel that this is not a problem in identification, as the narrow, elliptical (and sometimes erupted) glands are very diagnostic.

Quantification of identified and unknowns was accomplished by counting the fragments and then reducing the counts to a relative abundance scale, comparable to the 1–5 abundance scale used by other investigators. Our relative abundance scale is as follows 1: 1 fragment; 2: 2–25; 2.5: 26–50; 3: 51–75; 3.5: 76–100; 4: 101–200; 4.5: 201–300; and 5: >300 fragments. If a taxon was particularly abundant, up to 300 fragments were counted, as in the case of small cactus spines or mesquite leaves.

Pollen samples were extracted from all middens except RC4, RC4-14, and RC3, which were collected at an earlier date and vouchers were unavailable. A small indurated subsample (∼25 cc or 10–20 g) was removed from the original, cemented midden for pollen analysis, and 10 g were later separated and soaked in distilled water. This disaggregated subsample was screened through a 500 μm (No. 35) mesh screen. A 10% KOH solution was added to remove humic acids. HCl was used to remove carbonates and to dissolve the matrix of the *Lycopodium* spore tablets (batch No. 124961, Stockmarr, 1972) added to quantify differences in pollen concentration between the different middens. The residue was treated with HF to eliminate silica, acetolyzed, and then mounted in glycerine (Faegri and Iversen, 1989). Pollen slides were observed under a Leica Galen microscope, at 400× magnification.

Pollen determinations were based on pollen reference collections, illustrated atlases and published works on pollen morphology. A total of 68 different pollen types, mostly including family and genus levels, were identified in the Rough Canyon midden series. More than 300 pollen grains were counted per midden sample (mean of 342 pollen grains/sample, with a range of 313 to 466; the higher count was made to offset the overabundance of *Quercus* pollen in RC430F). An emphasis was also made to determine at least 20 pollen types per sample. The program GPALWIN (Goeury, 1998) was used to draw the pollen diagram. Pollen percentages of only selected taxa are presented; the complete pollen data may be accessed via the North American Pollen Database. The taxon Chenopodiaceae includes the pollen types Chenopodiaceae—*Amaranthus* and *Sarcobatus* (greasewood). Despite the stratigraphic discontinuity characteristic of midden records, we used pollen curves rather than bar graphs and treated the midden series as a semi-continuous record. We classified temporal pollen zones based on variations in the frequencies of the major taxa; these zones roughly coincide with variations in the plant macrofossil record. Interpretations of the pollen assemblages are based on published literature for the general southwestern US. There have been no systematic studies of modern pollen rain variations across elevational gradients in the northern Chihuahuan Desert, and such a study was beyond the scope of the Rough Canyon project.

5. Results

5.1. Radiocarbon dating

Table 2 reports the ^{14}C dates for the Rough Canyon middens, ranging from 17 300 to 200 ^{14}C yr BP. The sequence includes six middens of Pleistocene age (>11 000 ^{14}C yr BP), one early Holocene (10 540 ^{14}C yr BP), nine middle Holocene (8000–4000 ^{14}C yr BP), and 14 late Holocene (<4000 ^{14}C yr BP). In the text, tables and illustrations, we report all dates as uncalibrated radiocarbon ages (Table 2). Some of the midden assemblages have temporal mixing, which we tested by directly

dating potential contaminants. RC442B contains both abundant *Juniperus* sp. twigs and *Larrea tridentata* leaves. Fecal pellets were dated at 6295 ^{14}C yr BP, but *Larrea* leaves yealded a date of 3205 ^{14}C yr BP indicating that this juniper-creosotebush assemblage is actually mixed. Based on floral composition, we determined that RC-3 is also a mixed assemblage. This midden, which dates at 13 230 ^{14}C yr BP and is dominated by *Pinus edulis* and *Juniperus scopulorum*, was the only Pleistocene midden to also contain *Prosopis glandulosa*, *Larrea tridentata*, and *Fouquieria splendens*. In this case, we did not feel it necessary to date the different fractions. There may be other possible contaminants in our Pleistocene samples (RC4, RC4-14, RC3, RC436, RC444A and RC444C). Candidates include leaves of cf. *Viguiera stenoloba* in RC4 and RC436, and *Larrea tridentata* in RC444A and RC444CC, and achenes of *Flourensia cernua* in RC444A and *Parthenium incanum* in RC444A and RC444C. We also redated RC436 to test whether or not *Choisya dumosa* leaves and twigs actually date to the Pleistocene. *Choisya* occurs commonly in Pleistocene sediments in Pendejo Cave, Pleistocene through Holocene middens in Rough Canyon, and in the present-day Rough Canyon environment. An AMS date of 12 590 ^{14}C yr BP from RC436 agrees with the date on fecal pellets at 12 910 ^{14}C yr BP.

5.2. Plant macrofossil assemblages

Plant macrofossil assemblages are summarized in Fig. 4; the complete data set can be accessed online (http://climchange.cr.usgs.gov/data/midden/). Late glacial middens dating 12 900 ^{14}C yr BP or older are dominated by *Pinus edulis* and *Juniperus scopulorum*, with some representation of 'toothed' junipers (probably *J. coahuilensis* and/or *J. monosperma*). *J. scopulorum* was found in all of the late glacial middens except RC444A (11 820 ^{14}C yr BP) and 444C (11 680 ^{14}C yr BP). The latter two samples contained abundant juniper twigs with toothed scales, which may belong to either *J. monosperma* and/or *J. coahuilensis*. One of these samples only had pinyon shells and no needles. The site is a dry, west-facing cliff along the exposed Otero Mesa escarpment (Fig. 2). There is some ambiguity in that we cannot ascer-
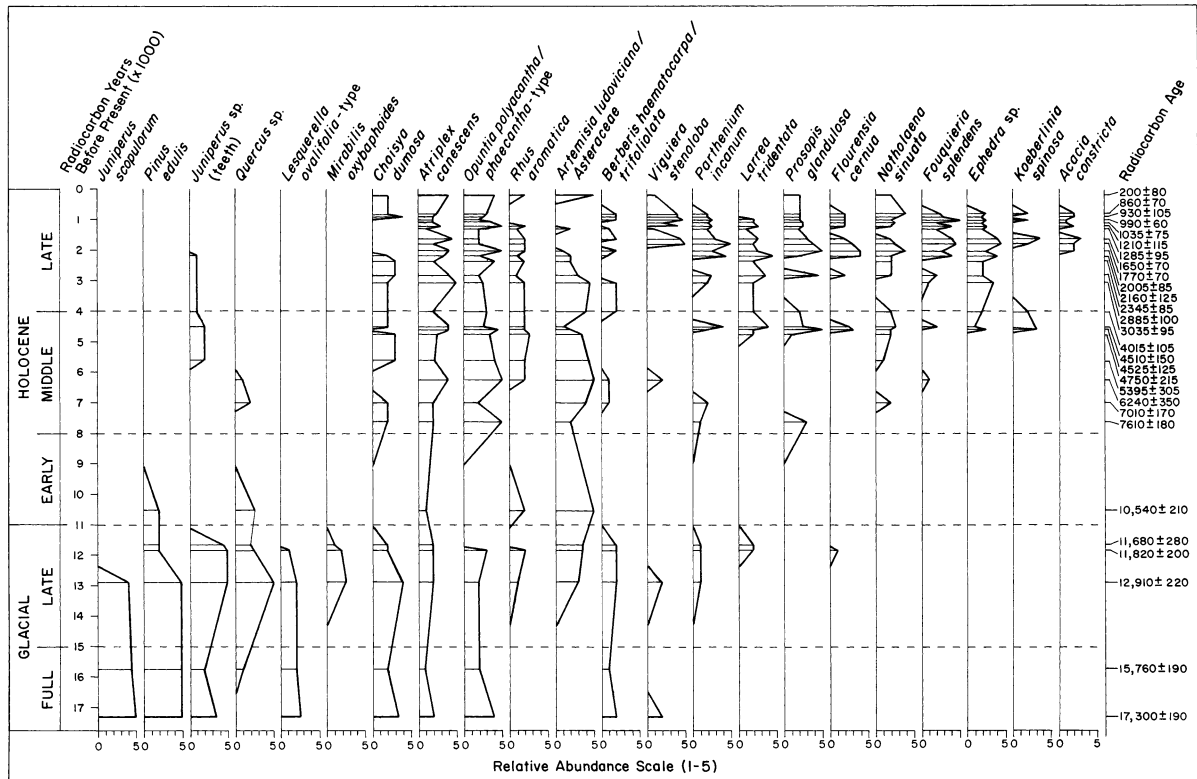
Fig. 4. Diagram of plant macrofossil abundance through time for select species from the Rough Canyon series.

tain whether *J. scopulorum* is absent, and *P. edulis* is scarce because the site is harsh or vegetation had actually changed by 11 800 ^{14}C yr BP. However, an assemblage (RC430C) dated to 10 540 ^{14}C yr BP not only lacks *J. scopulorum*, but also lacks any junipers and only contains pinyon shells that could have been carried several kilometers to the site by birds.

Other plants present in the Pleistocene middens but scarce or missing in the Holocene part of the chronology include oaks (*Quercus* spp.), *Lesquerella ovalifolia* (bladderpod), *Mirabilis oxybaphoides* (four-o'clock), *Physalis* (ground cherry) sp. and *Cercocarpus montanus* (mountain mahogany). Many species occur in both Pleistocene and Holocene middens, including *Choisya dumosa*, *Atriplex canescens*, *Bahia* sp., *Opuntia polyacantha/phaeacantha* type, *Rhus trilobata*, *Artemisia ludoviciana*, and *Berberis* spp. Some

of the plants with persistent records are cosmopolitan species with large genotypic variability across North America, specifically *Atriplex canescens*, *Opuntia polyacantha/phaecantha*-type, and *Rhus trilobata*. Although we cannot discriminate these genotypes morphologically, we suspect that in many cases, these seemingly persistent species actually represent genotypic replacement from the late glacial to the Holocene. An AMS date of 12 590 ^{14}C yr BP on the distinctive leaves of *Choisya dumosa* indicates that this cliffside plant, now restricted to north-facing, mesic slopes, occurred on dry southern and western exposures during the late glacial. Its ubiquity in Pleistocene sediments at Pendejo Cave indicates that it was also common on north-facing slopes. *Choisya dumosa* persisted on southern (RC435A) and western (RC444B) exposures into the late Holocene until ~2000 ^{14}C yr BP. We had difficulty in

discriminating between *Berberis haematocarpa* and *B. trifoliata*, both of which occur today along the Otero Mesa escarpment. *B. haematocarpa* extends into northern New Mexico, whereas *B. trifoliata* meets its northern limits in southern New Mexico. It is possible that the former is replaced by the latter in the Holocene, but we cannot discriminate between fragmentary remains of the two species.

There is general agreement between the floral assemblages in the Rough Canyon middens and Pendejo Cave sediments. Exceptions include the presence of *Pseudotsuga menziesii*, *Lithospermum* sp. and *Stipa neomexicana* in the Pendejo Cave sediments (J. Gish, unpublished data). While examining the exposed stratigraphy of the unexcavated portion of Pendejo Cave in 1996, we also noted *Pseudotsuga* needles and a large cache of *S. neomexicana* seeds. All three species are mesophytes that were probably restricted to the wetter, north-facing slopes of Rough Canyon.

Notable absences for the Pleistocene middens include *Ephedra* sp., *Eurotia lanata*, and *Artemisia tridentata*-type. Sagebrush was apparently unimportant in the Pleistocene middens. We found few leaves, and Rough Canyon middens lacked the shredded cambium (or wormwood) prevalent in modern and late Holocene middens on the Colorado Plateau, where sagebrush is dominant. We identified a few *Artemisia* cf. *bigelovii* (RC436) leaves, but there is no indication of a sagebrush understory in the Pleistocene pinyon–juniper woodland in Rough Canyon (see similar finding from pollen analysis described below). *Artemisia ludoviciana*, a common plant today in Rough Canyon, was not identified in the full-glacial middens (RC4 and RC414), is found in every midden from 13 230 ^{14}C yr BP to 2005 ^{14}C yr BP, occurs only sporadically after 2000 ^{14}C yr BP, and is dominant in a sample dated at 200 ^{14}C yr BP.

The middle Holocene middens in Rough Canyon are not particularly distinctive from the late Holocene ones. If we assume that traces of *Prosopis glandulosa*, *Viguiera stenoloba*, *Parthenium incanum*, *Larrea tridentata*, and *Flourensia cernua* are all Holocene contaminants in Pleistocene middens, then the Holocene can be defined as a time of sequential arrivals of desert shrubs and few departures. For example, *Prosopis*

glandulosa and *Parthenium incanum* appear first at 7610 ^{14}C yr BP, *Ephedra* sp., *Dalea formosa*, *Fouquieria splendens* and *Flourensia cernua* at 6295 ^{14}C yr BP, *Larrea tridentata* at 4750 ^{14}C yr BP, *Koeberlinia spinosa* at 4525 ^{14}C yr BP, and *Acacia constricta* at 2005 ^{14}C yr BP (*Acacia* pollen is first identified in the 2345 yr ^{14}C BP midden). The fern *Notholaena sinuata*, which typically grows on exposed limestone outcrops throughout the southern deserts, makes its first appearance in both the macrofossil and pollen records at 7010 ^{14}C yr BP (it was also found in the mixed Pleistocene/Holocene assemblage of RC3).

5.3. Pollen profile

The summary pollen diagram for Rough Canyon is presented in Fig. 5. Three major pollen zones are identified. Zone 1, from 12 910 to 10 540 ^{14}C yr BP, is characterized by up to 60% Cupressaceae (*Juniperus*) and *Quercus*, from 0 to 20% *Pinus*. A comparison of surface and midden pollen assemblages in the Sonoran Desert (Anderson and Van Devender, 1991) showed that *Pinus* tends to be under-represented in middens relative to modern surface samples. This may explain low pollen frequencies of *Pinus* compared to macrofossil abundance in middens before 11 000 ^{14}C yr BP. Low grass (Poaceae) pollen percentages (<5%) characterize Zone 1.

The high (86.9%) *Quercus* pollen frequencies at 10 540 ^{14}C yr BP could be due to anthers being introduced directly into the midden by packrats; both tetrads and clumps of *Quercus* pollen grains were observed in this sample. *Quercus* macrofossils are also recorded in this sample (Fig. 4). The lack of *Juniperus* pollen (and macrofossils) and low *Pinus* pollen percentage in this sample suggest that extirpation of pinyon–juniper woodland was accomplished by at least 10 540 [14]C.

Zone 1 lacks diversity with no sample producing more than 20 taxa. In the Holocene (Zones 2 and 3), only RC430D (6240 ^{14}C yr BP) had less than 20 taxa. *Larrea* pollen grains were found in the three late glacial samples (12 590, 11 690, and 11 680 ^{14}C yr BP), two of which also contained traces of *Larrea* macrofossils. The macrofossils did not weigh enough (>1 mg) to permit AMS dating.
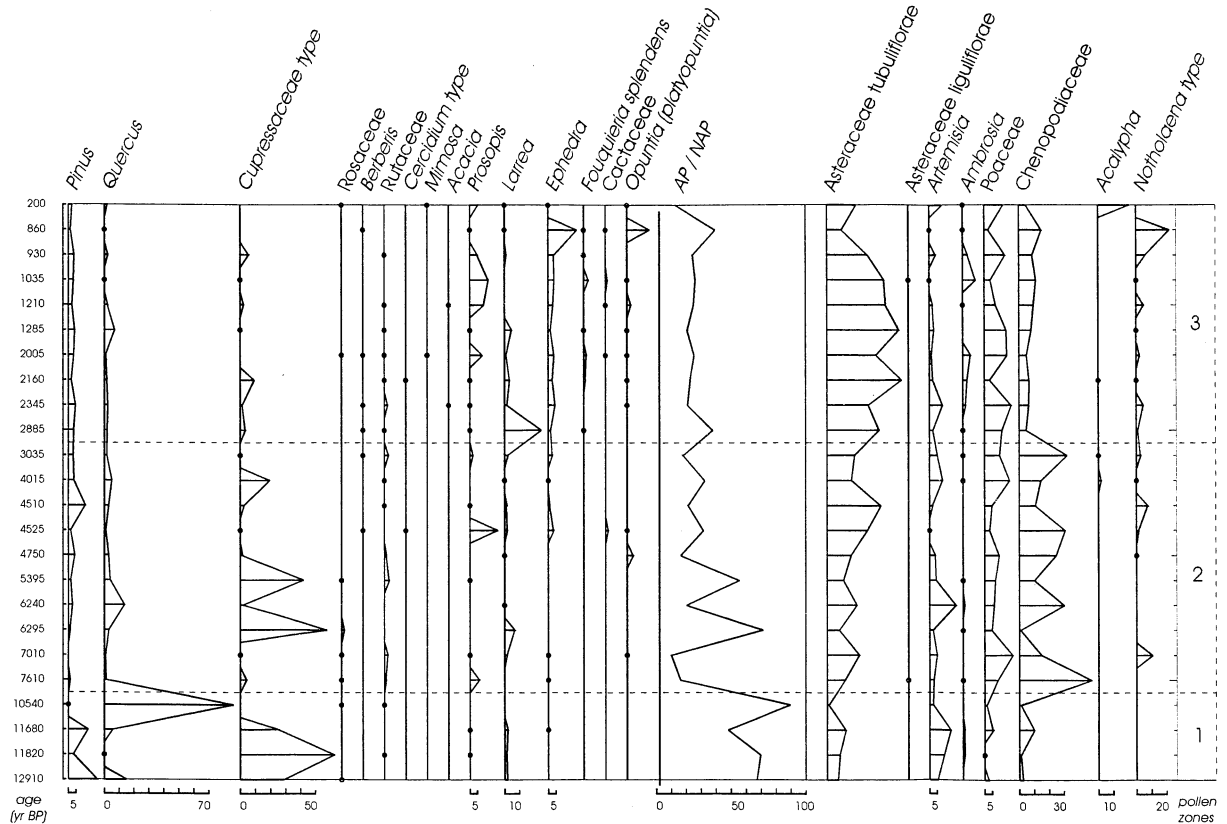
Fig. 5. Diagram of pollen abundance through time for select species from the Rough Canyon series.

Larrea pollen is represented erratically throughout the Holocene and was not identified from middens dating 10 640, 7610, 7010, 5395, 1210, 1035 ^{14}C yr BP. *Prosopis* pollen was also identified from samples dated 11 680 and 11 820 ^{14}C yr BP.

Samples from 7610 to 200 ^{14}C yr BP, included in zones 2 and 3, are dominated by non-arboreal pollen. Lower frequencies of Cupressaceae (*Juniperus*), *Quercus* and *Pinus* pollen suggest that most of the tree pollen is regional, though introduction of pollen cones from local, isolated junipers could explain higher Cupressaceae pollen percentages at 2160, 4015, and 5395 ^{14}C yr BP. Over-representation of Cupressaceae pollen at levels disproportionate with their role in local vegetation has been demonstrated by Thompson (1985). From 7610 to 3035 ^{14}C yr BP (Pollen Zone 2), Chenopodiaceae, Asteraceae tubuliflorae, *Artemisia*, and Poaceae are dominant. A high variance between the samples is mostly explained by the changing percentages of Cupressaceae, which decreases in frequency during the late Holocene. The main feature of Zone 2 is the dominance of Chenopodiaceae. From around 4525 to 3035 ^{14}C yr BP, the first pollen records of *Ephedra*, Cactaceae, and *Acacia* as well as higher pollen frequencies of Asteraceae Tubuliflorae-type indicate initial modernization of the local flora.

Increased Asteraceae–Tubuliflorae, *Ambrosia*, and *Ephedra* pollen frequencies, and decreases in Chenopodiaceae and *Artemisia* characterize the late Holocene from 2885 to 200 ^{14}C yr BP (Pollen Zone 3). In addition, *Opuntia* (platyopuntia; probably *O. violacea* and *O. polyacantha/phaeacantha*-type), other Cactaceae, *Fouquieria splendens*, *Prosopis*, *Acacia*, and *Mimosa* attain their highest frequencies in the latest Holocene. Those pollen spectra reflect essentially modern local vegetation.

Moderate pollen frequencies of Poaceae (5–20%) suggest that grasses may have become more important locally after 10 000 ^{14}C yr BP; note that grasses generally tend to be under-represented in midden pollen relative to surface samples from the nearby environment (Anderson and Van Devender, 1991).

Evidence of a progressive vegetation change is evident in the transition from the Middle to Late Holocene transition, ~4500 ^{14}C yr BP, marked by the arrival of new desert species. A second transition occurs ~3000 ^{14}C yr BP with increases in local desert shrubs and the change from Chenopodiaceae to Asteraceae-dominated pollen spectra. The ratio of arboreal to non-arboreal pollen changed little throughout the Holocene.

6. Discussion

The late glacial vegetation of Rough Canyon during the last glacial period was pinyon–juniper woodland dominated by *P. edulis*, *Juniperus scopulorum* and *J. monosperma*/*J. coahuilensis*. This is consistent with records of pinyon–juniper woodlands at desert elevations (<1700 m) at midden sites throughout the northern Chihuahuan Desert, from the Sevilleta LTER south to the Big Bend of the Rio Grande and the Bolson de Mapimi, Coahuila (Wells, 1987; Van Devender, 1987, 1990a; Betancourt et al., 1993; Lanner and Van Devender, 1998). What is unique about our record is the resolution it affords in reconstructing the exact elevational and latitudinal limits of the dominant species. *Pseudotsuga* needles identified from Pendejo Cave sediments probably came from one or a few scattered trees in what was mostly pinyon–juniper woodland. The absence of *Pseudotsuga* in Pleistocene middens from the drier, south-facing side of the canyon opposite Pendejo Cave indicates that, regionally, this tree's lower limit was ~1490 m on north-facing, limestone slopes. Full glacial middens from the Sacramento Mountains (Van Devender et al., 1984) indicate that *Pseudotsuga* extended down to at least 1555 m on south-facing, limestone slopes.

Lanner and Van Devender (1981) identified most of the Pleistocene pinyon remains in the Hueco Mountains 50 km south of Rough Canyon as *Pinus remota*. This pinyon currently has a restricted distribution in west Texas and Coahuila, but during the glacial period, it was the dominant tree in pinyon–juniper woodlands south of the Huecos. Some of the needles in the Hueco samples also were referred to *P. edulis*. If the Hueco Mountains material is indeed *P. remota* and the Rough Canyon *P. edulis*, then we have identified intersection of their two ranges, and a possible zone of Pleistocene hybridization, along the Otero Mesa Escarpment between the Huecos and Rough Canyon. This hybridization eventually may be recognized in genetic markers preserved in ancient DNA extracted from the pinyon needles.

The presence of *J. scopulorum* in Rough Canyon provides tighter control on its regional elevational limits, and may explain the absence of its close competitor, *J. deppeana*, during the glacial period. In general, these two species tend to have mutually exclusive ranges (Fig. 6). *J. scopulorum* occurs from British Columbia to as far south as the Sierra Madre Occidental, where it is often mistaken with *J. flaccida*. In the Southwest, it is often thought of as a riparian species, though north of 34°N, it is co-dominant with *Pinus edulis* and *P. ponderosa* above 2200 m. *J. scopulorum* is co-dominant with *P. flexilis* in the foothills of the central and northern Rockies. *J. scopulorum* is ubiquitous in glacial-age middens above 1490 m from the northern Chihuahuan Desert, across the Colorado Plateau and portions of the Great Basin (Betancourt et al., 1990), with an unusual record at 975 m in Organ Pipe National Monument on the Arizona–Sonora border (Van Devender, 1990b). On limestone substrates along the Otero Mesa escarpment, *J. scopulorum* reached its lower limits between 1490 and 1430 m, occurring in glacial-age middens in the Guadalupe, Sacramento, Rough Canyon, and even one midden at 1495 m in the Hueco Mountains (RW4028: 13 200 ± 450 ^{14}C yr BP; N31 42′36″N, W105 59′22″W).

Today, *Juniperus deppeana* is the common juniper above 2000 m in southern New Mexico/southern Arizona and northern Mexico. Its northern limits narrowly overlap the southern limits of *J. scopulorum*, e.g. *J. scopulorum* replaces *J. deppeana* as the dominant juniper in the ecotone
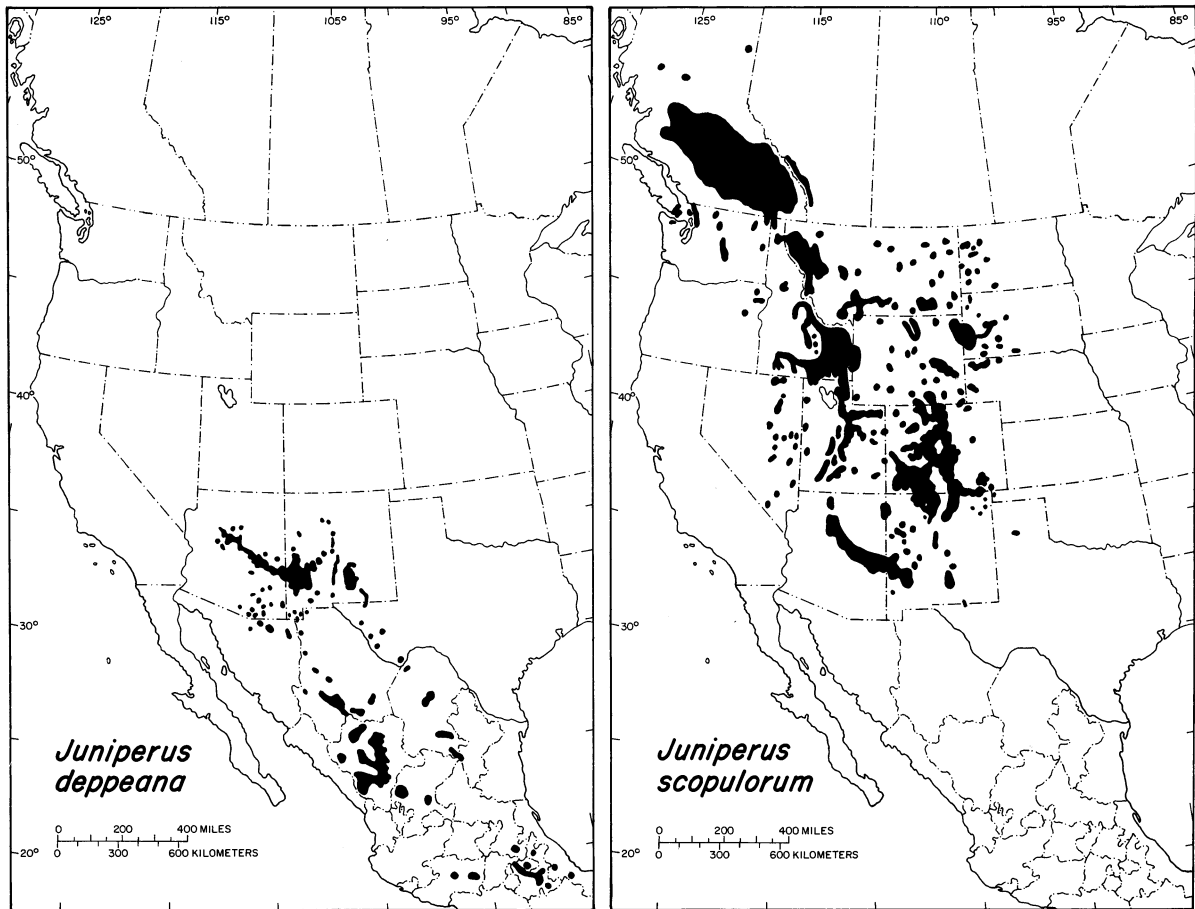
Fig. 6. Modern distribution of Rocky Mountain juniper *Juniperus scopulorum* and alligator bark juniper *Juniperus deppeana* (from Little, 1971). *J. scopulorum* is ubiquitous in late Pleistocene middens above 1490 m from the northern Chihuahuan Desert, across the Colorado Plateau and portions of the Great Basin, with an unusual record at 975 m in Organ Pipe National Monument on the Arizona–Sonora border (Van Devender, 1990b). Because the two junipers tend to have mutually exclusive ranges, the southern distribution of *J. scopulorum* during the Pleistocene would have truncated the northern distribution of *J. deppeana*. At present, *J. deppeana* has yet to be identified from Pleistocene middens in the United States. It is likely that the distribution of *J. deppeana* north of Mexico is entirely a Holocene phenomenon.

between ponderosa pine and pinyon–juniper woodlands from the southern to the northern end of the San Agustin Plains. If the two junipers had mutually exclusive ranges during the late glacial as they do today, the southern distribution of *J. scopulorum* during the Pleistocene would have truncated the northern distribution of *J. deppeana*. At present, *J. deppeana* has yet to be identified from Pleistocene middens in the United States. It is likely that *J. deppeana* has occurred north of Mexico only during the Holocene. We note that,

unlike *J. scopulorum*, *J. deppeana* tends to develop false rings due to a secondary surge in growth when the monsoonal rains break the arid foresummer. Also, *J. deppeana* is a sprouter and well adapted to fire. Both false rings and sprouting suggest that *J. deppeana* is adapted to arid foresummers followed by mid-to-late summer rains.

The comparison between Rough Canyon and the Hueco Mountains series also resolves the geographic limits for other species. *Glossopetalon spinescens* and *Mortonia sempervivens* (sandpaper

bush) occur in the Hueco but not in the Rough Canyon middens, suggesting that the Hueco populations represent their northern limits. Likewise, *Choysia dumosa* must have been at or near its northern limits in Rough Canyon during the late Pleistocene; today, its northern limits are in southern Socorro County ~ 100 km to the north. In the Sacramento Mountains, *Choysia dumosa* was missing from two Pleistocene middens (18 300 and 16 260 ^{14}C yr BP) but dominant in an early Holocene midden dated at 10 590 ^{14}C yr BP (Van Devender et al., 1984). Because the glacial and early Holocene middens are from two different canyons, we cannot rule out that northern limits extended north of Rough Canyon into the Sacramento Mountains during the glacial period. *Choysia* reproduces asexually and is toxic to game and livestock (Benson and Darrow, 1981). Cloning could have allowed *Choysia* to maintain its northern limits throughout the late Quaternary conditions, free from the stricter conditions needed for sexual reproduction. The same clone could have persisted for thousands of years. Fossil leaves of *Choisya dumosa* in Pleistocene sediments and middens may represent the same stock as clones currently growing at the mouth of the cave. Advances in molecular approaches may eventually allow determination of individuals (clones) from ancient DNA. *Choysia*'s toxicity would have released it from the added pressure of browsing by large herbivores, many of them which became extinct at $\sim 11\,000$ [14]C yr BP.

The glacial-age midden record is equivocal about the type of vegetation growing on deeper soils between 1400 and 2000 m in southern New Mexico. Both *Artemisia* and Poaceae are poorly represented in Zone 1 midden pollen from Rough Canyon. Middens from elsewhere in the northern Chihuahuan Desert generally lack sagebrush (*Artemisia tridentata*-type species) macrofossils and/or contain only low frequencies of Artemisia pollen (Van Devender 1990a). Other studies have inferred that *Artemisia* steppe expanded south into the middle Rio Grande/Tularosa Basin, or that these areas were dominated instead by C_4 grasslands.

Today, sagebrush dominates open terrain west of Santa Fe/Taos above 1980 m, whereas C_4 grass-

lands dominate the eastern foothills of the Rockies at similar elevations. A shift 2–4° shift south and 500 m lower would have displaced sagebrush steppe down to the middle Rio Grande Basin, Hueco Bolson, and Tularosa and Salt Basins during the glacial period. Indirect evidence includes the presence of animals presently associated with sagebrush communities, including *Centrocarpus urophasianus* and *Lagurus curtatus* in Pleistocene cave faunas at Isleta, Dry and Pendejo Caves (Harris and Findley, 1964; Harris, 1987). One possibility is a patchy distribution of sagebrush steppe in southern New Mexico, with two tongues extending into the southern High Plains and along the Continental Divide near the Arizona–New Mexico border separated by grasslands (Art Harris, personal communication).

Evidence for summer-flowering C_4 grasslands dominating deeper soils in the middle Rio Grande Basin, Tularosa Basin and Hueco Bolson comes from combined pollen analysis (Monger et al., 1998), $\delta^{13}C$ of soil carbonates in buried soils in the Tularosa/middle Rio Grande Basin (Cole and Monger, 1994; Monger et al., 1998; Buck, 1996) and $\delta^{13}C$ tooth enamel of large herbivores at Pendejo, Isleta, Howell's Ridge, Dry, U-Bar, and Sandia Cave (Connin et al., 1998). The carbon isotopic evidence for both soil carbonates and tooth enamel indicates enriched values consonant with C_4 grass dominance. The pollen evidence is less clear, with only one of the glacial soils exhibiting grass percentages ($\sim 30\%$) above Holocene values (Monger et al., 1998).

Contradictory evidence for C_4 grass dominance, at least for the late glacial, comes from carbon and nitrogen isotopes of bison bone collagen from the Lubbock Lake site, where Stafford et al. record a shift in average $\delta^{13}C$ values from $-17\permil$ ($> 70\%$ C_3 grasses) at 12 000 ^{14}C yr BP, $-15\permil$ (55% C_3 grasses) at 10 000 ^{14}C yr BP, $-10\permil$ (75% C_4 grasses) at 5000 ^{14}C yr, and $-8\permil$ (90–95% C_4 grasses) at 500 ^{14}C yr BP. $\delta^{15}N$ values were most positive when C_3 species dominated and least positive when C_4 species dominated; Stafford et al. (1994) interpreted this to mean decreasing soil moisture from years 12 500 to the present. Lubbock Lake is only 300 km northeast of Rough Canyon, and raises the possibility that the interpretations of soil carbonate/tooth

enamel or the bison bone collagen are wrong, or that there was a steep boundary in summer rainfall regimes and C_3/C_4 ratios in grasslands of the southern Basin and Range and southern High Plains.

We are unsure about the exact climatic significance for the glacial occurrence of *P. edulis* and *J. scopulorum* in rocky environments above 1490 m in southern New Mexico, the long-term stability of northern limits for plants such as *Choisya dumosa*, and the possible glacial dominance of C_4 grassland in the open spaces of Otero Mesa and the Tularosa Basin. Part of this uncertainty comes from knowledge that lake levels oscillated greatly in nearby pluvial lakes, including Lakes Sacramento (Wilkins and Currey, 1997) and Otero (Hawley, 1993), with shorelines within tens of kilometers and only 100–200 m below Rough Canyon and other midden sites in the area. Wilkins and Currey (1997) have identified Lake King highstands at 22 570, 19 090, 17 180 and 15 940 ^{14}C yr BP, which correlate with highstands in Lakes San Agustin (Phillips et al., 1992) and Estancia (Allen and Anderson 1993). The midden record is stratigraphically discontinous, but nevertheless gives the appearance that vegetation trends during the last glaciation were monotonous, rather than punctuated by dramatic, millennial scale variability. Mixtures of plants that do not occur today (e.g. *Juniperus scopulorum* and *Choysia dumosa*) could have resulted at least partly by displacing the modern climate of northern New Mexico into the limestone-dominated landscapes of the northern Chihuahuan Desert. Exact modern analogs for glacial plant communities in Rough Canyon are difficult to find in New Mexico. Nevertheless, modern climate at the lower end of pinyon–juniper woodlands dominated by *J. scopulorum* must be roughly similar to glacial climates in Rough Canyon. In New Mexico, extensive *P. edulis–J. scopulorum* woodlands now are common above 2100 m in the upper Pecos River Basin, east of Santa Fe, New Mexico. Mean annual precipitation (MAP) at Pecos (2106 m) is 407 mm, only 20% more than at Rough Canyon. The mean July maximum temperatures are only 3.5°C cooler at Pecos than at Rough Canyon. One consideration is whether a 3.5°C summer cooling and 20%

increase in MAP would be sufficient to sustain pluvial lakes in the Tularosa and Salt Basins.

The only closed basin where *P. edulis–J. scopulorum* currently dominate the edge of the basin is the northern San Agustin Plains ($\sim$2000–2100 m), which supported a large pluvial lake during the last glacial period (Markgraf et al., 1984; Phillips et al., 1992) but today holds no permanent water. Pietown (2425 m) on the northern edge of the San Agustin Plains has a July T°max of 27.7°C and MAT of 399 mm, or $\sim$5°C cooler in summer and 20% wetter than Rough Canyon. To explain pluvial lakes, we can only surmise that glacial summers were disproportionately cooler and perhaps cloudier, and that cool season precipitation was greater, was spread over a longer portion of the year, came more in the form of snowfall, and was less variable from year to year than today. Upper air flow divergence of a strengthened jet stream aloft across the southern edge of the Laurentide ice sheet may have parked a south branch of the jet stream $\sim$20° south of its present winter (January) position (45°N) (Bartlein et al., 1998), which would have supplied more winter precipitation to the region. It is unclear what role the tropical Pacific might have played in modulating the mean latitudinal position of the polar jet stream and the strength of the subtropical jet stream. Today, the amount of cool season precipitation in the southwest depends in part on the year-to-year variability in the position and sinuosity of the upper-air westerlies and alternation between El Niño (wet) and La Niña (dry) episodes. The fact that pluvial lake levels oscillated during the LGM suggests a sensitive hydrological balance and a variable winter storm track.

Several explanations are possible for the hypothesized prevalence of C_4 grasslands in southern New Mexico. Low atmospheric pCO_2 levels could have shifted the competitive balance from C_3 shrubs and grasses to C_4 grasses, which do not photorespire and thus can fix carbon efficiently in low pCO_2 environments (Cole and Monger, 1994). Alternatively, effective summer moisture may have been greater than today due to reduced maximum temperatures and/or higher rainfall in the early or late summer (Connin et al., 1998). Some combination of low pCO_2 levels and summer rainfall

patterns could have limited sagebrush and favored C_4 grasslands. A modern, floristic analog in southeastern Colorado, where *P. edulis*/*J. scopulorum* woodlands merge with short-grass (*Bouteloua gracilis*) prairie, is not inconsistent with reduced aridity during the foresummer and greater rainfall throughout the summer. Monsoonal circulation, however, should have been weaker during glacial summers for physical reasons, including greater and more persistent snowcover in the southern Rockies and Colorado Plateau suppressing continental heating, cooling of tropical and subtropical waters, and presumed displacement of the polar jet stream in summer by the Laurentide ice sheet, blocking seasonal, northward migration of the Bermuda High (see Connin et al., 1998 for more detail).

The Holocene record for Rough Canyon duplicates similar midden sequences from the area, showing departures of woodland species in the early Holocene and sequential arrival of desert shrubs during the middle and late Holocene. One important difference is the early departures of pinyons and junipers at Rough Canyon, compared to the Hueco Mountains and other key sites throughout the southern deserts. However, this may be an artifact of sample density with little duplication of middens in the 12 000– 10 000 ^{14}C yr BP range and no samples dated between 10 000 and 8000 ^{14}C yr BP.

Traces of *Larrea* and *Prosopis* pollen, and of *Larrea tridentata*, *Flourensia cernua*, *Viguiera stenoloba*, *Parthenium incanum*, and *Dalea formosa* macrofossils, in late glacial middens is troubling. These early occurrences of desert elements either represent temporal mixing or suggest that these taxa were present in the local or regional vegetation at a time when pinyon–juniper woodlands dominated rocky environments between 600 and 1700 m throughout the Chihuahuan Desert. Insufficient macrofossil weight (and insufficient funds) prevented AMS dating of macrofossils to test for contamination of macrofossil assemblages with younger material, and we simply cannot date the pollen. Temporal mixing in pollen assemblages probably is a common phenomenon and may be evident in identification of two Sonoran Desert species in three of the middens. *Simmondsia* pollen

was found in a sample 1210 ^{14}C yr BP and *Cercidium* type in middens dated at 4625 and 2005 ^{14}C yr BP. Both pollen types are distinctive, and we are confident about their identification. The eastern ranges of both taxa stop in western Arizona (Turner et al., 1995), ca 400 km from Rough Canyon, and macrofossils of neither taxon have been identified from northern Chihuahuan Desert middens. The most likely explanation is that pollen contamination occurred during subsampling at the Desert Laboratory in Tucson or in processing at the pollen lab in Hermosillo. Both laboratories are surrounded by Sonoran Desert vegetation. For Chihuahuan Desert species, however, we cannot rule out that their occurrence in midden pollen assemblages represents their actual presence in the late glacial vegetation of Rough Canyon and the Tularosa Basin. In several midden studies where both macrofossils and pollen have been analyzed, first appearances of southern species tend to be earlier in pollen than macrofossil assemblages (King and Van Devender, 1977; Thompson, 1985; Davis, 1990; Anderson and Van Devender, 1991; Betancourt et al., 1991). One explanation is that these species appear in the regional vegetation long before they are registered in the very local floras around midden sites. The inability to discriminate between contamination and first appearances, particularly in pollen assemblages, continues to be a weakness of midden studies.

Both the plant macrofossil and pollen record from Rough Canyon middens reflect gradual immigration of desert shrubs into the northern Chihuahuan Desert during the middle and late Holocene. We suspect that late arrivals may be related not to migrational distances but rather to the gradual erosion of Pleistocene soils during the Holocene, exposing large areas of limestone bedrock (Van Devender, 1990a,b). This may be reflected in the progressive increase of *Notholaena*, a fern commonly found on limestone outcrops, and in Asteraceae (e.g. *Flourensia*, *Parthenium* and *Viguiera*) in both the pollen and macrofossil records.

The pollen profile (Fig. 5) shows a striking shift in dominance from Chenopodiaceae in the middle Holocene to Asteraceae Tubuliflorae in the late

Holocene. Interpretation of Chenopodiaceae/ Asteraceae Tubuliflorae-type pollen ratios in middens presents different challenges than in lake deposits. The midden chenopod pollen from the Rough Canyon series probably came from two sources: (1) halophytic species in the salt flats >10 km west of Rough Canyon (*Sarcobatus*, *Salicornia*, *Allenrolfea*, *Suaeda*, *Chenopodium* and *Atriplex*); and (2) shrubs (*Atriplex canescens* and *Ceratoides lanata*) and herbs (*Chenopodium*) growing locally on rocky hillslopes in Rough Canyon. There is no permanent water currently in the floor of the Tularosa Basin, but temporary lakes form during particularly wet seasons and years. A reduction in Chenopodiaceae pollen from middle into late Holocene could signify a general drop in the water table or a decrease in seasonal ponds and lakes. Alternatively, the drop in Chenopodiaceae and increase in Asteraceae Tubuliflorae indicate more local changes on the hillslopes in Rough Canyon. Some of the chenopod macrofossils could not be identified to species in the Rough Canyon series, but the prevalent material is from *Atriplex canescen*s and *Ceratoides lanata*. Increases in the frequency of *Ceratoides lanata* would suggest wetter winters, and increases in the frequency of *Atriplex canescens* could be linked to a variety of phenomena, including seasonally fluctuating water tables in lowlands and increased levels of disturbance on hillslopes. *Atriplex canescens* is common in Pleistocene 'woodland' middens from the northern Chihuahuan Desert (Van Devender, 1990a). In contrast, the most likely species to contribute significantly to Asteraceae Tubuliflorae frequencies in late Holocene of Rough Canyon are *Gutierrezia* spp., *Viguiera stenoloba*, *Flourensia cernua* and *Parthenium incanum*. The latter three plants are all typical Chihuahuan Desert species that grow commonly on limestone and increase perceptibly during the late Holocene in the midden records. Hence, an increase in Asteraceae Tubuliflorae could be interpreted as increasing aridification, either through decreasing effective moisture or long-term erosion exposing more and more limestone bedrock.

In the southwestern USA, there is abundant evidence for pervasive hydrological (winter) drought during the middle Holocene, with a variety of lakes drying up from the Great Basin (Thompson et al., 1993) to the hot deserts of the southwestern USA (Davis and Shafer, 1992; Anderson, 1993; Blinn et al., 1994; Hasbargen, 1994; Weng and Jackson, 1999). Also, the middle Holocene represents a hiatus in packrat middens throughout the southwestern USA. One explanation is that midden production at a regional scale tracks the performance of woody perennials, which respond primarily to winter moisture (Spaulding, 1991; Betancourt et al., 1993). The middle Holocene was also a time of accelerated geomorphic change. Badland formation in the Cretaceous and Tertiary shales of the southern Colorado Plateau appears to have accelerated during the middle Holocene (Wells et al., 1990). Also, on the southern High Plains, more geomorphic change occurred in the Altithermal than any other period during the late Quaternary, including valley aggradation, surface deflation and dune build-up (Holliday, 1989).

Some authors argue that the middle Holocene was a time of greater summer rainfall in the southwestern USA. For example, Fall's (1997) reconstruction of the subalpine and montane lower forest borders suggests that central Colorado received slightly more summer precipitation between 9000 and 4000 yr BP than today. This agrees with isotope evidence from the San Juan Mountains in southern Colorado (Friedman et al. 1988). Van Devender (1995) and McAuliffe and Van Devender (1998) infer from midden evidence that an enhanced monsoon supported modest expansions of the perennial C_4 grass *Setaria* spp. (bristlegrass) into the upper edges of Arizona Upland desertscrub in the northeastern Sonoran Desert in Arizona and Sinaloan thornscrub in northeastern Sonora. In the Sonoran Desert, there is also evidence for shifts in the topographic position of key plants. Woody legumes such as *Cercidium*, *Acacia* and *Prosopis* occurred on dry slopes at sites where they are presently restricted to watercourses. Episodes of downcutting (arroyo formation) occurred in southern Arizona (Waters, 1985, 1988) and elsewhere in the Southwest between 7000 and 5500 yr BP. These events could have been caused by a period of high-intensity summer storms. The contemporaneity of arroyo

cutting events at century resolution, however, is not possible. Interestingly, many desert shrubs arrived in the northern Chihuahuan Desert after 4000 yr BP. Shrub expansion could have been forestalled by higher summer precipitation and greater grass cover and ultimately enhanced by the general stripping of the soil mantle, which exposed large surfaces of limestone bedrock.

7. Conclusions

Late Quaternary environments of the northern Chihuahuan Desert in south-central New Mexico and west Texas are well known, compared to most other arid regions of North America. New information, such as the Rough Canyon midden series' can now be interpreted in rich paleohydrological and paleoecogical contexts. This series replicates patterns and trends from other midden records in the northern Chihuahuan Desert, while providing new insights on shifting plant distributions since the LGM. During the glacial period, rocky terrain at what are now desert elevations (<1900 m) supported extensive pinyon–juniper woodlands, while deeper soils supported summer-flowering (C_4) grasses. These grasslands were grazed by now-extinct horses and camels that are well represented in the Pendejo Cave fauna (Harris, 1995).

Montane conifers (*Pseudotsuga menziesii*, *Picea pungens*, *Pinus ponderosa*, *Abies concolor*) graded into pinyon–juniper woodland down to ∼1490 m elevation, typically on north-facing canyon slopes (Van Devender and Toolin, 1983; Van Devender et al., 1984; this report). The upper limits of pinyon–juniper woodland were ∼1800 m on limestone and probably lower on other substrates. Woodlands dominated by *Pinus edullis* and *Juniperus scopulorum* at 1490 m in Rough Canyon blended into woodlands dominated by *Pinus remota, Pinus edulis* and *Juniperus monosperma/J. coahuilensis* in the Hueco Mountains, only 50 m lower and 50 km south. Several plants present in the Hueco Mountains but absent at Rough Canyon, including *Pinus remota* and *Glossopetalon spinescens*, met their northern limits on limestone along the Otero Mesa escarpment. Glacial-age records of *Choisya dumosa* in Rough Canyon may

represent long-lived clones at or near their northern limits. Such clones could have persisted as individuals well into the Holocene. Species that must have been displaced far south of their modern ranges include not just desert elements, but also some woodland species such as *Juniperus deppeana*.

Holocene warming and/or drying could have started as early as 12 000 ^{14}C yr BP in Rough Canyon, based on the absence of *Juniperus scopulorum* and reduced abundance of *Pinus edulis* in two samples dated at 11 800 and 11 650 ^{14}C yr BP. Interestingly, this is about the time when packrat activity and rates of sedimentation decrease abruptly in Pendejo Cave (Chrisman et al., 1996). This contradicts the prevailing view (summarized in Betancourt et al., 1990, 1993; Van Devender, 1990a,b) that southwestern vegetation changed abruptly at 11 000 ^{14}C yr BP, rather than as a series of steps beginning before 11 000 ^{14}C yr BP. One possible explanation is the poor resolution in the radiocarbon timescale during this transitional period (Bartlein et al., 1995).

During the Holocene, the sequential arrival of desert elements at Rough Canyon (1490–1530 m) closely parallels other nearby midden records from the Hueco (1270–1495 m), Sacramento (1555–1690 m), and San Andres (1520–1705 m) Mountains. Trace amounts of macrofossils in late glacial middens of some desert elements such as *Larrea tridentata*, *Flourensia cernua*, *Viguiera stenoloba*, *Prosopis*, *Parthenium incanum*, and *Dalea formosa* may be Holocene contaminants. If so, this suggests that contamination of macrofossil assemblages is more common than generally accepted by midden researchers. AMS dating of all of these trace occurrences was beyond the scope of the present study and should be resolved at a later date. Desert elements are also represented as pollen in late glacial assemblages, raising the question of whether they indicate temporal mixing in middens or first arrivals. Because traces of midden pollen cannot be AMS-dated, first arrivals based on midden pollen evidence can neither be dismissed out of hand nor taken at face value; they remain a matter of interpretation.

One of the salient features of the Rough Canyon midden series is the late Holocene dominance of desert elements in both the macrofossil and pollen

assemblages. This dominance may in part reflect slow, postglacial migration from populations far to the south. Local increases in densities of many Chihuahuan Desert elements, specifically in the Asteraceae, however, may have been enhanced by Holocene erosion of relict soils (developed under glacial woodlands) and progressive exposure of limestone bedrock.

Acknowledgements

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